

SNOW COVER AND THE *DIAPENSIA LAPPONICA*
HABITAT IN THE WHITE MOUNTAINS,
NEW HAMPSHIRE¹

WESLEY N. TIFFNEY, JR.

The alpine zones of the White Mountains, New Hampshire, provide a convenient study area for investigators interested in the ecology of alpine plants. The White Mountains are a series of peaks, heavily glaciated during the Pleistocene Epoch, 46 of which exceed 4,000 ft. The highest of these is Mt. Washington (6,288 ft.) in the Presidential Range. During the Wisconsin substage of Pleistocene glaciation the climate allowed arctic plants to become established in the area. The present harsh climate typical of the alpine zones of the White Mountains has maintained these plants as an arctic outpost in a temperate area. Treeline, here defined as the upper limit of continuous tree cover, is located at about 4,800 ft. on the west side of the Presidential Range and at about 5,200 ft. on the east (Antevs, 1932; Bliss, 1963). Prevailing winds are from the west. The best developed alpine zone in the White Mountains is found on the Presidential Range; it extends from Mt. Madison (5,363 ft.) in the north to Mt. Clinton (4,312 ft.) in the south. The area is about eight miles long and two miles wide at its greatest extent and encompasses about 7.5 square miles (Bliss, 1963). A smaller alpine zone exists in the Franconia Range some 20 miles west of the Presidential Range; it extends from Mt. North Lafayette (5,000 ft.) to Mt. Haystack (4,600 ft.), having as its highest point Mt. Lafayette (5,249 ft.). This zone encompasses about 1.5 square miles.

The climate of the alpine zone has been summarized by several investigators (Antevs, 1932; Bliss, 1963; Pease, 1964). Weather information has been gathered by the Mt.

¹This paper constitutes a part of a doctoral dissertation submitted to the University of New Hampshire.

Washington Observatory located on the summit of that peak. In general, the climate is characterized by high winds, low temperatures, high precipitation with heavy winter snow and extensive fog and cloud cover.

This paper represents a portion of a larger investigation involving the distribution of White Mountain plants relative to winter snow cover. The purpose of the present study is to define the ecological relationship between snow cover and a habitat typified by *Diapensia lapponica* L., an Angiosperm cushion-forming plant, used by Bliss (1963) to characterize the association he termed the "*Diapensia* community".

In both the arctic and in the alpine zones of the White Mountains *Diapensia* is reported in exposed and wind-swept areas (Antevs, 1932; Hadley and Bliss, 1964; Löve and Löve, 1966; Courtin, 1968, 1968a). Several investigators have further suggested that the plant is limited to areas blown clear of winter snow (Hadley and Bliss, 1964; Courtin, 1968, 1968a). Bliss (1963) reports that *Diapensia lapponica* is a prime colonizer of bare ground and is found in ". . . areas that are subjected to frost action because of the lack of winter snow cover". Later, (1966) he reports, "*Diapensia* communities are found where winter snow cover is thin, or non-existent, and melts early in spring". Bliss (1969) recorded snow depth for two winters in three locations; it is not stated if any of these locations were in *Diapensia* areas. However, he states, "During much of the winter, large areas of Alpine Garden are blown free of snow, areas dominated by *Diapensia* communities".

My objective in this study was to analyze the species composition of the *Diapensia* habitat and to determine the degree of interdependence among its component species. First, it was necessary to test the snow cover hypothesis described above by gathering extensive records of winter snow depths in *Diapensia* habitats. I observed a number of habitats over several seasons to find if the plants did inhabit snow-free areas and if these areas were substantially free of snow throughout the winter season. A

system of summer sampling was designed to accumulate data for statistical analysis of interdependence among component species of the habitat.

Snow Depth and Winter Dessication

For the winter snow depth study 14 plots were established and marked with wire stakes at the margins of the greatest *Diapensia* concentrations. Two plots were located in each of the following areas: near the fourth peak of Mt. Adams, at the Lake-of-the-Clouds Hut, on the summit cone of Mt. Washington, on the section of the Chandler Ridge termed Cape Horn, at the lip of Huntington Ravine in Alpine Garden, at Lion Head in Alpine Garden and at Cow Pasture on the Automobile Road. These plots were visited throughout the winters of 1966-1967, 1967-1968 and 1968-1969 on as nearly a regular basis as the harsh winter weather of the Presidential Range permitted. Each plot was visited at least once each winter and some as many as eight times. During the three winters 14 trips were made to check snow depths in plots.

After a snowfall in the White Mountains the wind frequently rises, usually from the west. Most of the snow which has accumulated during the storm in the open alpine zone is blown away and collects below treeline on the east side of the mountains. This is particularly true on the Presidential Range and leads to the massive accumulations of snow common in the large glacial valleys on the east side of the range, such as Tuckerman and Huntington Ravines. Snow remaining in the alpine zone is packed into the sparse vegetation or in the lee of large wind obstructions. In ascending the mountain increasing snow depth is encountered until treeline is reached; above treeline snow cover conforms to the microrelief of the alpine zone. In the *Diapensia* habitat there are few obstructions and virtually all the snow is blown clear throughout the winter season (Fig. 1).

A trip to check snow depth made on February 19-26, 1967, will serve as an example of the snow cover/wind

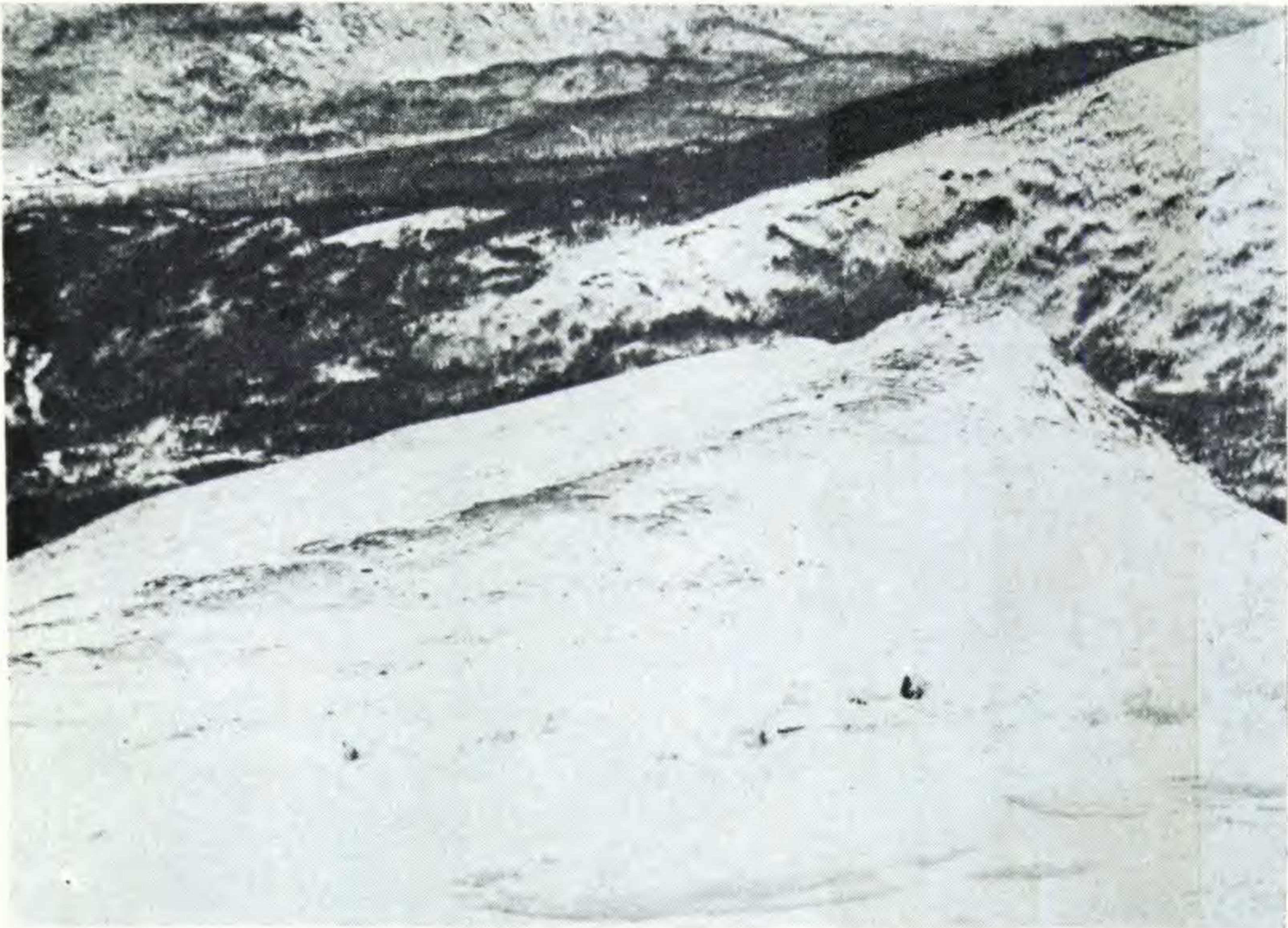


Fig. 1. Snow-free ridge crest, about one-half mile long, near Lion Head in Alpine Garden, Presidential Range, New Hampshire. The area is dominated by *Diapensia lapponica*. March 3, 1969.

relationship on the Presidential Range. On the night of February 20 a storm deposited a recorded 2.7 inches of snow at the summit of Mt. Washington. Drifts of two to three feet accumulated in the vicinity of the Weather Observatory. On the morning of February 21 the wind rose from the west and reached a sustained velocity of 60 to 70 MPH with a peak gust of 105 MPH. Virtually all the snow, including the large drifts, was removed from the summit area. On February 23-24 another storm developed and deposited a recorded 19 inches of snow at the summit. Winds rose during the evening of February 24 and reached a sustained velocity of 70 to 80 MPH. The wind persisted through February 26. Again, almost all accumulated snow was removed from the summit area. Visits to six *Diapensia* habitats on February 26, varying from 6,000 to 4,000 feet elevation, showed that all were devoid



Fig. 2. Winter aspect of a *Diapensia* habitat at Cape Horn, Chandler Ridge, Mt. Washington. Surrounding areas are covered with snow. The ice axe is about 40 inches long. Feb. 26, 1968

of snow after a total fall of 21.7 inches over the previous six days (Fig. 2).

Late wet snowfalls, although more dense than dry mid-winter snows, are also blown away by strong winds and do not accumulate in the *Diapensia* habitat nor do they delay flowering. On May 26, 1967, a 12.8 inch snowfall was followed by winds of 70 MPH. Visits to several habitats on May 30 and 31 disclosed no snow in the areas. Less than three weeks later on June 18, 1967, *Diapensia* plants were in full bloom throughout the Presidential Range (Fig. 3).

Winds are not as strong where plants are actually growing on the range as they are where recorded on a 39 foot instrument tower on the summit of Mt. Washington. A wind velocity of 100 MPH on the summit is equivalent, on the average, to a speed of 30 MPH at plant level (Courtin,



Fig. 3. Plants of *Diapensia lapponica* in bloom, Cape Horn, Mt. Washington, New Hampshire. June 17, 1968. The lateral area covered by the photograph is about 18 inches long.

1968). Such wind velocities are still sufficient to remove snow from exposed areas and to promote desiccation in winter-exposed plants.

In an average winter on Mt. Washington the Weather Observatory records 221.4 inches of snow. The winter of 1966-1967 totaled 260.6 inches, the winter of 1967-1968, 211.1 inches and the record winter of 1968-1969 yielded 566.4 inches of snow. These variations in annual snowfall have little effect on the total amount of snow adhering to the ground in the alpine zone. My observations indicate that the snow holding capacity of the zone is reached early in the winter. Additional snow is blown away by strong winds. This study spanned two relatively normal snowfall years and one record year. Amounts of snow in *Diapensia* habitats and other areas checked remained constant. This minimal snow cover melts rapidly once warm weather arrives and melts at about the same time each year. Even

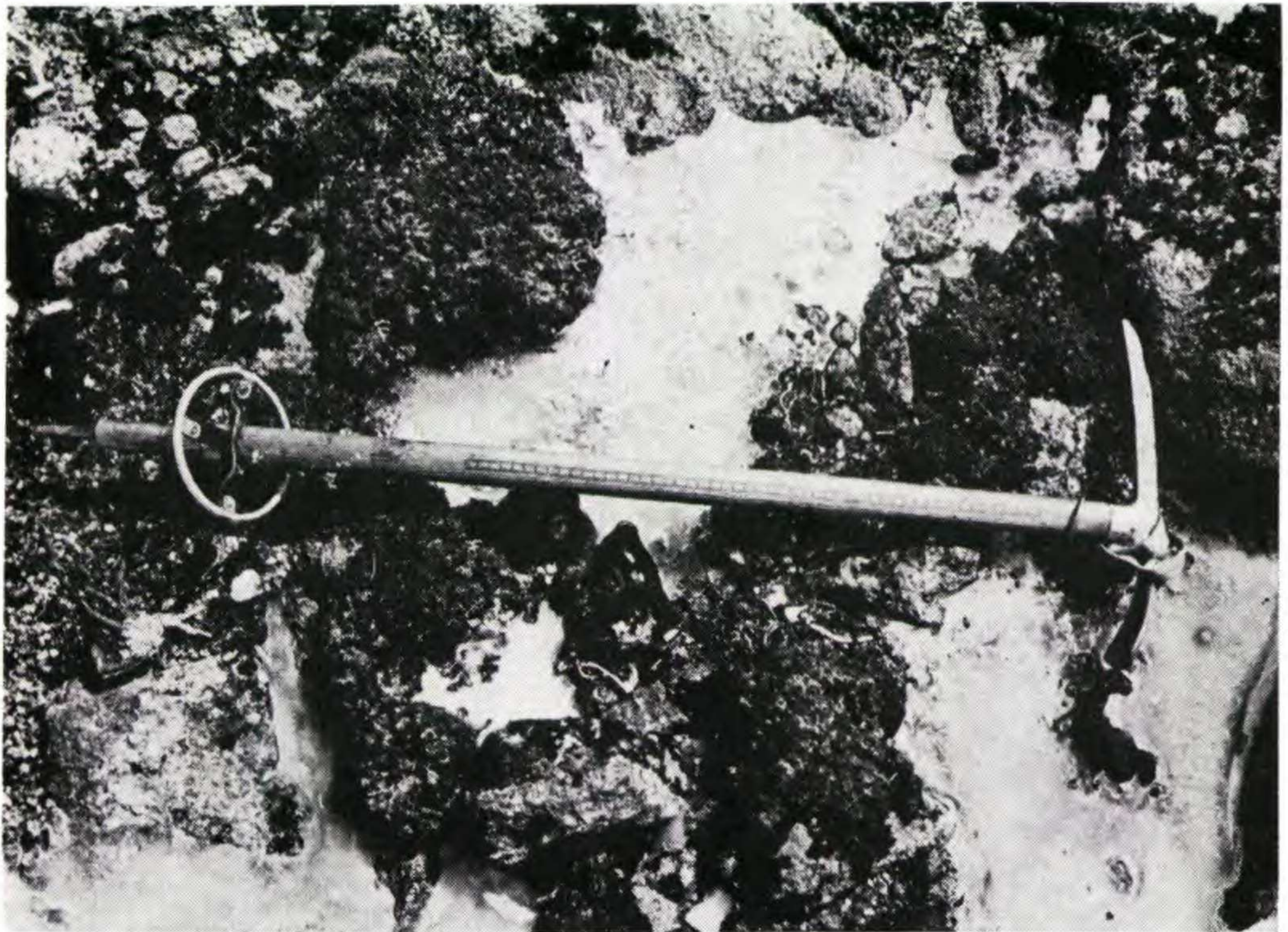


Fig. 4. Winter condition of *Diapensia lapponica* plants, Cape Horn, Chandler Ridge, Mt. Washington, New Hampshire. Meltwater has formed ice about the bases of the plants but the crowns are fully exposed. Jan. 26, 1967. The ice axe is about 40 inches long.

late-lasting drifts supporting specialized snowbank communities (Bliss, 1963) disappear at about the same time each season. The flowering time of *Diapensia lapponica* and other spring-blooming plants on the Presidential Range is not greatly influenced by heavy or light snow years or by heavy snowfalls late in May. In the three years included in this study alpine plants were at the peak of their bloom between June 15 and June 25 (Fig. 3).

The examples above, drawn from the winter of 1966-1967, are typical of results of other visits in 1967-1968 and 1968-1969. In some cases meltwater had formed ice about the bases of *Diapensia* plants but in all cases observed the major portion of the plant was exposed (Fig. 4). Areas dominated by *Diapensia* were those areas blown clear of snow throughout the winter. Accumulations of as little as a few inches of snow marked the margin of the *Diapensia*

habitat and the beginning of a transition to another form of plant cover.

Desiccation is a major factor in the distribution of alpine plants as Tranquillini (1964) notes when he states, "Extremely short snow cover can only be tolerated by plants that are resistant not only to cold but also to long periods of drought . . .", and Sakai (1970) notes that ". . . desiccation damage in winter constitutes the greatest limiting factor for growing plants in cold climates and in high mountains . . .". Plants in the *Diapensia* habitat appear well suited to resist the effects of desiccation. Several investigators have noted that the low mat or cushion form exhibited by plants such as *Diapensia* is of survival value in these conditions (Holttum, 1922; Hadley and Bliss, 1964; Courtin, 1968a). The low profile of these plants offers less resistance to strong winds and their desiccating effect is minimized.

Information on the freezing resistance of several plants of the *Diapensia* habitat has been accumulated by Sakai and Otsuka (1970). They note that several species acquire a resistance in the fall at -15° C. that allows them to withstand winter temperatures of -70° C. After acquiring such resistance *Vaccinium uliginosum* could withstand temperatures of -50° C., *V. vitis-idaea* and *Loiseleuria procumbens* could survive at -70° C. The most cold resistant plant tested was *Diapensia lapponica* which, after full hardening, could survive immersion in liquid nitrogen at -196° C. (Sakai and Otsuka, 1970). The lowest recorded temperature for Mt. Washington is -44° C. (-47° F.).

Species Composition

Twenty-two *Diapensia* habitats were chosen for sampling to determine species composition and major sample areas were located in them. Plots were placed in the center of the habitat. The sampling procedure used is similar to that of Bliss (1963). An area 4 by 8 meters (320,000 sq. cm.) was marked with surveying tape and stakes. The 4-meter axis was located parallel to the slope of the ground.

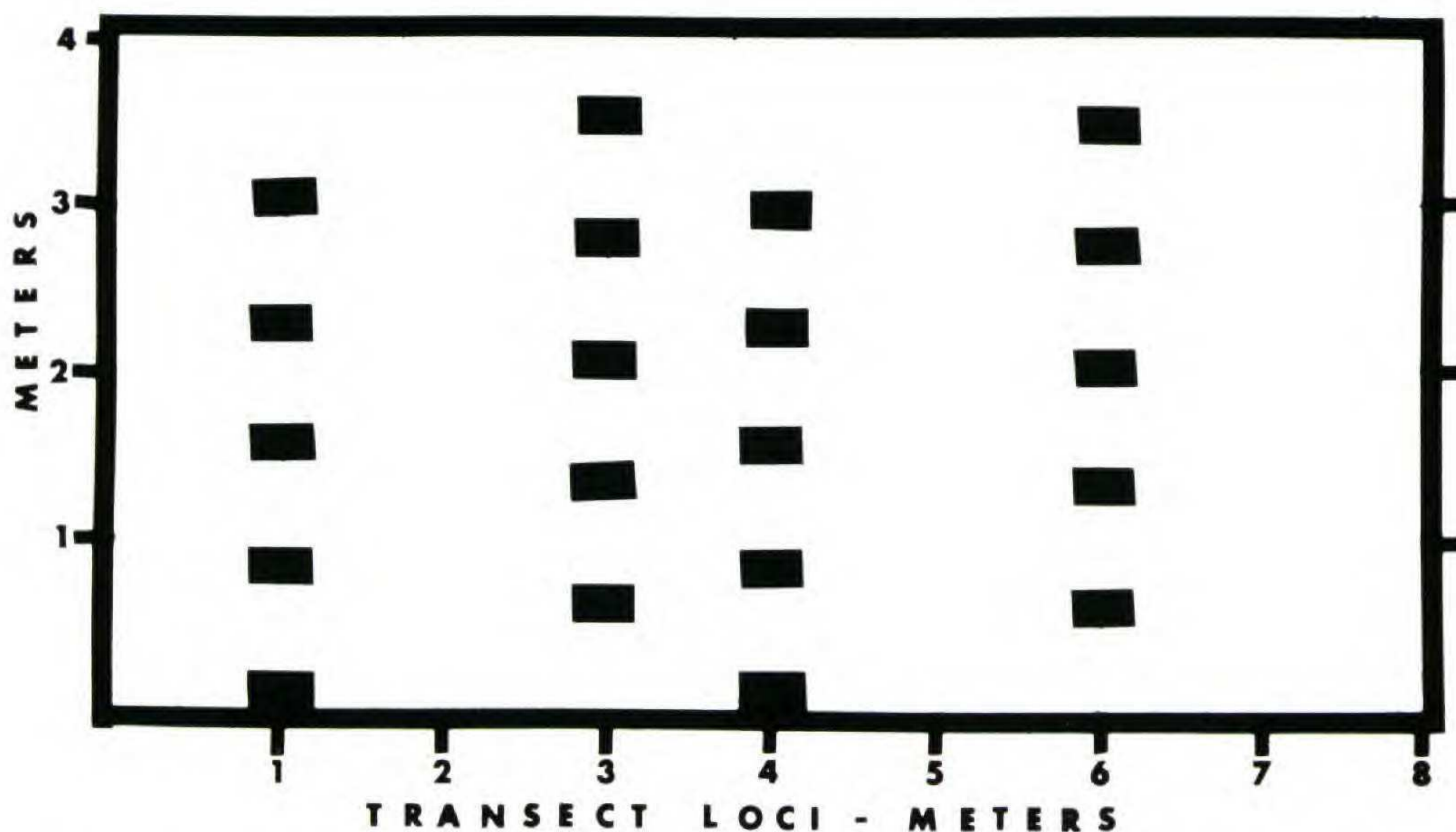


Fig. 5. Arrangement of quadrats within a major sample area. The transects on which the quadrats are located are randomly chosen. The design is similar to that of Bliss (1963).

Five rectangular quadrats 25 by 40 cm. (1,000 sq. cm.) were established along a sequence of transects based at four randomly chosen locations on the 8-meter axis. Alternate quadrat transects were begun on the 8-meter axis, and others 0.5 meters from it. Twenty rectangular quadrats were established in each major sample area for a total sampled area of 20,000 sq. cm. or 6.3% of the total area sampled (Fig. 5). Quadrat size and number corresponded with recommendations for plot size and sample design in alpine vegetation made by Eddleman et al. (1964).

Measurements were taken of the ground area covered by all vascular plants in each 25 by 40 cm. quadrat. Measurements were taken also for cover of moss and lichen and for uncolonized ground and rock. These were expressed as percent cover for each sample area, and grand totals for all 22 areas sampled were compiled. Areas sampled for species composition were, in general, the same as those used for winter observations. Results are given in Table 1.

My results expressed as percent cover are roughly comparable to those of Bliss (1963) expressed as importance

Table 1

<u>Type</u>	<u>Mean</u>	<u>Range</u>	<u>Standard Deviation</u>
Rock	31.1	1.4-66.6	19.5
<i>Diapensia lapponica</i>	27.6	1.8-54.0	15.0
Lichen (all types)	13.0	0-46.4	14.1
<i>Vaccinium uliginosum</i>	5.8	0-18.5	5.2
<i>Juncus trifidus</i>	5.3	0-23.0	6.4
Uncolonized Ground	4.3	0-18.2	4.6
Moss (all types)	3.2	0-31.1	6.7
<i>Carex bigelowii</i>	3.1	0-11.8	3.6
<i>Salix uva-ursi</i>	1.5	0-7.9	2.5
<i>Vaccinium vitis-idaea</i>	1.1	0-7.2	2.0
<i>Potentilla tridentata</i>	1.0	0-4.8	1.3
<i>Loiseleuria procumbens</i>	0.8	0-7.8	1.9
<i>Rhododendron lapponicum</i>	0.6	0-4.3	1.1
<i>Arenaria groenlandica</i>	0.5	0-2.5	0.7

Results of sampling major plant components of the *Diapensia* habitat, White Mountains, New Hampshire. Means, ranges and standard deviations for all types sampled are expressed as percent ground cover of the total area sampled.

Other plants were present in quantities of less than 0.5%; these minor components were not subjected to statistical analysis. These were, together with their means: *Solidago cutleri* 0.4%; *Poa alpigena* 0.3%; *Scirpus cespitosus* var. *callosus* 0.2%; *Betula* ssp. 0.1%; *Vaccinium angustifolium* 0.05%; *Abies balsamea* 0.05%; *Empetrum nigrum* 0.03%; *Prenanthes boottii* 0.01%; and *Lycopodium selago* 0.002%. These minor forms totaled 1.1% of the total area sampled. The nomenclature used is that of Fernald (1950).

values. He recorded higher values for rock and uncolonized ground as well as for *Juncus trifidus*; slightly higher values for *Potentilla tridentata*, *Loiseleuria procumbens*, *Rhododendron lapponicum*, and *Arenaria groenlandica*; similar values for *Diapensia lapponica* and *Vaccinium uliginosum*, and a lower value for lichen. Results of Bliss's analysis are based on 2 to 9 sample areas.

Results of my sampling indicate that 47.3% of the area in the *Diapensia* habitats was occupied by vascular plants, 35.4% was occupied by rock and uncolonized ground and 16.2% by moss and lichen. The typical plant of these habitats was *Diapensia lapponica* which was about five times as concentrated as the next ranking vascular plant.

Wide ranges and large standard deviations were found for all component species tested (Table 1). This suggests that it is not possible to predict with accuracy the concentrations of the components to be found in a given *Diapensia* habitat. The minimum concentration of *Diapensia lapponica*, 1.8% of the area sampled, was encountered in a plot located on the west flank of Mt. Madison. Other sample plots placed in nearby *Diapensia* habitats yielded results of 30.1%, 35.0% and 47.2% cover of *D. lapponica*. The maximum concentration encountered, 54.0% was in a plot located on the west side of Mt. Lafayette in the Franconia Range. Nearby sample plots in this area showed concentrations for *D. lapponica* of 15.6%, 22.0% and 33.4%. Values for other component species of the habitat were equally variable.

Analysis of Component Species

To assess the degree of interdependence existing among the component species of the *Diapensia* habitat statistical testing was necessary. Tests based on frequency data such as the "C_s" correlation of Hurlbert (1969) were rejected due to the difficulty of collecting accurate frequency data in alpine vegetation. As Woodin (1959) has indicated, frequency information is difficult to obtain in alpine areas of mat-form vegetation as it is hard to tell where one plant

ends and another begins. Goodall (1970) notes that, "Many plants, however, have methods of vegetative reproduction which make distinctions between individuals highly arbitrary. Biomass per unit area is a measure which is more consistently objective". For these reasons estimates of biomass in terms of percent ground cover were used here. The purpose of this part of the study is to assess the degree of interdependence present among plants of the *Diapensia* habitat. Sokal and Rohlf (1969) have said, ". . . when we wish to establish the degree of association between pairs of variables in a population sample, correlation analysis is the proper approach." Hence, the product-moment correlation coefficient has been used here.

In computing the correlation coefficient, data are ranked in two sets. The first set (Y_1) is arranged in increasing rank order, the second set (Y_2) is paired with the first. The correlation coefficient (r) indicates the degree of association between the two sets (Y_1 and Y_2) and may be expressed in percent. The value of r may vary from -1 (minus 100%) to $+1$ (plus 100%). A value approaching -1 indicates negative association between Y_1 and Y_2 , a value approaching $+1$ indicates positive association between the two sets of variables. A value of r approaching 0 indicates little interdependence between Y_1 and Y_2 . Reciprocal tests yield the same results. For each correlation coefficient (value of r) significance tests are performed against the hypothesis that $r = 0$.

Each of the 14 major species components of the *Diapensia* habitat (those having means greater than 0.5% of the total area sampled) was tested against the other 13 major components. This required a total of 91 correlation coefficient tests, which were performed with the aid of a computer and using Leasco Systems and Research program no. CL-00001.023-00. Results are given in Table 2.

Ninety-one tests were performed; only eight yielded positive or negative correlation coefficients of 50% or greater. The strongest relationship observed was between moss and *Arenaria groenlandica* with a value of 68.0%.

Table 2

	Rock	<i>Diapensia lapponica</i>	Lichen	<i>Vaccinium uliginosum</i>	<i>Juncus trifidus</i>	Uncolonized Ground	Moss	<i>Carex bigelowii</i>	<i>Salix uva-ursi</i>	<i>Vaccinium vitis-idaea</i>	<i>Potentilla tridentata</i>	<i>Loiseleuria procumbens</i>	<i>Rhododendron lapponicum</i>
<i>Diapensia lapponica</i>	-23												
Lichen	-66	-24											
<i>Vaccinium uliginosum</i>	-20	-56	61										
<i>Juncus trifidus</i>	-25	-54	33	24									
Uncolonized Ground	-27	18	-32	-24	8								
Moss	-29	-4	-13	5	-19	10							
<i>Carex bigelowii</i>	-7	-14	-12	-34	-7	4	25						
<i>Salix uva-ursi</i>	23	-2	23	12	-21	-7	-30	-34					
<i>Vaccinium vitis idaea</i>	-27	19	20	-15	1	2	-15	-6	-32				
<i>Potentilla tridentata</i>	-24	-20	12	-13	15	-9	22	45	-13	9			
<i>Loiseleuria procumbens</i>	10	-22	-15	7	40	39	17	-27	-15	-11	0		
<i>Rhododendron lapponicum</i>	-19	-7	18	-7	16	7	-15	6	0	18	-20	-23	
<i>Arenaria groenlandica</i>	-29	2	-24	-12	-17	54	68	61	-5	-36	27	11	0

Results of the correlation coefficient test (values of r) for each major component of the *Diapensia* habitat (those having means greater than 0.5% of total area sampled) with every other major component of the habitat. Results are expressed as percent interdependence of Y_2 with Y_1 . The probability that the null hypothesis, $r = 0$, is true is .05 (5.0%) for values of r of 43% or greater.

None of the relationships tested could be considered strong (in excess of 90%).

A negative correlation coefficient resulted from the test between rock and lichen (-66%). Hence, rock and lichen covary negatively 66% of the time. Lichens sampled in this study were of the foliose and fruticose types. Crustose or rock-inhabiting forms were rare and were not included. A rock habitat is not suitable for the growth of lichens in the areas tested. With the exception of the negative relationship with lichens mentioned here, the large quantities of rock present in the *Diapensia* habitat (31.1% of the total area sampled) do not greatly influence the plants growing in the habitat.

Negative correlations resulted from tests of *Diapensia lapponica* with *Vaccinium uliginosum* (-56%) and with *Juncas trifidus* (-54%). This indicates that *D. lapponica* is negatively associated with *V. uliginosum* and *J. trifidus* about 55% of the time. The latter two plants are component species of an aggregation termed the "dwarf-shrub-rush-heath community" by Bliss (1963). This aggregation is commonly found at the margins of the *Diapensia* habitat. As these margins are reached snow cover increases slightly and *V. uliginosum* and *J. trifidus* begin to dominate. These two species also characterize areas of slightly greater snow cover, as in the lee of small obstructions dispersed throughout the *Diapensia* habitat itself. A gradient was established by Bliss (1963) with *Diapensia* at the snow-free extreme and the snowbank community at the other extreme. "Dwarf-shrub-rush-heath" is placed next in order with increasing snow cover to the *Diapensia* aggregation on this model. Rather than indicating that competitive exclusion is operating among *D. lapponica* and *V. uliginosum* and *J. trifidus*, I conclude that the negative correlations indicate that the margin of the *Diapensia* habitat has been reached in these sample situations and that a change to dominance by other forms is occurring. In this case the optimum snow cover situation for *Diapensia* has

been exceeded, and the optimum for the other two species is being approached.

This situation poses some possibilities for future experimental work. Snow depth in selected *Diapensia* habitats could be increased artificially by erecting several windbreaks in the habitat. Vegetation could be mapped prior to establishing windbreaks, then re-mapped in successive growing seasons. At question would be changes in the composition of plant aggregates growing in the altered habitat. A project of this nature is planned.

The test between *Vaccinium uliginosum* and lichen yielded a positive correlation of 61%. This indicates positive interdependence between *V. uliginosum* and lichen 61% of the time. Lichens, lacking roots, are not as firmly anchored as other plants and are frequently blown away by strong winds, an occurrence noted also by Antevs (1932). Most plants in the *Diapensia* habitat are mat-forming or cushion plants. An exception is *V. uliginosum* which, particularly in areas of slightly greater snow cover, adopts a more upright stature. Under these conditions *V. uliginosum* consists of a number of interwoven branches which provide anchorage for lichens. Possibly, the vascular plant provides support for lichens of several types and prevents them from being blown away by strong winds.

Positive results were obtained from tests between *Arenaria groenlandica* and uncolonized ground (54%), and moss (68%) and *Carex bigelowii* (61%).

The "sedge-meadow community" of Bliss (1963) was composed of two vascular plants, *Carex bigelowii* and *Arenaria groenlandica*. In addition to keeping snow cover records for the *Diapensia* habitat I accumulated information on winter snow depth in areas of sedge meadow on the summit cone of Mt. Washington. About one to two inches of snow accumulate in these areas, the rest being blown away. This amount is sufficient to cover the ground level meristems of *C. bigelowii*, although dead culms from the previous growing season frequently protrude from the thin snow cover. Sedge meadow occupies a similar posi-

tion on the snow cover gradient to the "dwarf-shrub-rush-heath community" of Bliss (1963). It is a marginal form to the *Diapensia* habitat, being supported by slightly increased snow depth. Again, experimental work should be performed to see if this form increases in concentration as a result of induced increases in snow cover in selected *Diapensia* habitats. *Carex bigelowii* and *A. groenlandica* are associated about 60% of the time in my samples.

There is doubt as to whether *Arenaria groenlandica* is annual or perennial (Gleason and Cronquist, 1963). The plant is described as being associated with mossy areas by Antevs (1932) and is regarded as being an early colonizer of bare ground by Antevs (1932) and by Bliss (1963). The plant is noted as growing on disturbed ground and particularly in hiking trails by Harris (1964). An annual or biennial life cycle would offer some explanation for the affinities of this plant for mossy areas and areas of open ground. In my tests it was positively associated with uncolonized ground 54% of the time and with moss 68% of the time. Open ground provides space to grow in the alpine zone otherwise occupied by perennial plants or rock. Mossy areas may promote seed germination and seedling survival due to greater water availability. Observations made in this study indicate that *A. groenlandica* is little controlled by snow cover, being distributed widely in a number of habitats which show wide variation in their amount of winter snow.

Loiseleuria procumbens is a cushion-forming plant very similar in form to *Diapensia lapponica*. It is rarely found in other than *Diapensia* habitats in the White Mountains. But, the test of *L. procumbens* with *D. lapponica* yielded a correlation coefficient of only -22% indicating that the plants were negatively associated -22% of the time. This value of r (-22%) is not significantly different from 0 at the .05 (5.0%) confidence level.

Of ten vascular plants tested (Table 2) five showed association with other vascular plants. These were *Diapensia lapponica*, *Vaccinium uliginosum*, *Juncus trifidus*,

Carex bigelowii and *Arenaria groenlandica*. One of these five, *V. uliginosum* covaried with lichen and one, *A. groenlandica*, showed interdependence with moss and with uncolonized ground. One group of non-vascular plants, lichens, covaried with rock. Five vascular plants showed no interdependence with other components of the habitat. These were *Salix uva-ursi*, *Vaccinium vitis-idaea*, *Potentilla tridentata*, *Loiseleuria procumbens* and *Rhododendron lapponicum*. Of ninety-one potential positive or negative interactions tested only eight occurred; none of these eight could be considered intense.

Discussion

The community concept involves the ideas that there are interactions among the component plants of the community and that the species structure of the community follows some predictable pattern. As Odum (1971) has said, "Communities not only have a definite functional unity with characteristic trophic structures and patterns of energy flow but they also have compositional unity in that there is a certain probability that certain species will occur together". Both Savile (1960) and Bliss (1962) have noted that competition in severe habitats is often secondary to the effects of the physical environment. The result ". . . may be the random occurrence of plants with few distinct associations" (Bliss, 1962). Savile (1960) suggests that arctic vegetation may better be described by habitats than by associations. I have used the term habitat, here defined as the place where a plant grows, in this analysis of an area dominated by *Diapensia lapponica*.

Sakai (1970) has noted that winter desiccation is a major limiting factor to alpine plant growth. Sakai and Otsuka (1970) have shown that *Diapensia lapponica*, *Vaccinium uliginosum*, *V. vitis-idaea* and *Loiseleuria procumbens* can survive very low temperatures. I suggest that *Diapensia* and other plants associated with it can survive in this snow-free and exposed habitat because they can tolerate very low temperatures and resist desiccation from strong

winter winds. Other plants are excluded because they are not adapted to survive in this harsh physical environment. Further investigation may provide more information on such relationships in the alpine zone.

Conclusions

The occurrence of the *Diapensia* habitat is predictable in relation to winter snow cover. *Diapensia lapponica* is found in areas blown clear of snow throughout the winter season. Increasing snow cover results in increasing dominance by other forms of plants. The *Diapensia* habitat is located at one extreme of the snow cover gradient, and this study suggests that aggregations characterized by *Vaccinium uliginosum*, *Juncus trifidus* and *Carex bigelowii* may be next in rank with increasing snow cover.

Wide variation was found among concentrations of all species components over the 22 habitats tested. These habitats do not consist of predictable percentages of species components.

Interdependence among the species components of the *Diapensia* habitat are few. Of ninety-one potential interactions tested eight occurred at significant levels and none of these could be considered intense. Control in the habitat is primarily exercised by the harsh microclimate. Prime factors are low temperatures and high winds combining to promote severe winter desiccation in this snow-free area. Plants which are able to survive in this harsh microenvironment do so and grow here. Others are not fitted to survive in these conditions and may be excluded by the microenvironment.

The unpredictable concentrations of plants in the areas tested, together with their lack of interactions, renders the use of the term habitat more appropriate than the term community to describe the aggregate found in this location.

Acknowledgements

I should like to give particular thanks to Dr. Albion R. Hodgdon for his continued support of this work. Thanks

are also due to the Mt. Washington Observatory for providing living facilities; and to S. Tiffney, M. Carriker, J. Roughgarden and J. Davis for their discussion and assistance.

LITERATURE CITED

- ANTEVS, E. 1932. Alpine zone of the Mt. Washington Range. Merrill and Webber Co., Auburn, Maine. 118p.
- BLISS, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. *Arctic* 15: 117-144.
- . 1963. Alpine plant communities of the Presidential Range, New Hampshire. *Ecology* 44: 678-697.
- . 1966. Plant productivity in alpine microenvironments on Mt. Washington, New Hampshire. *Ecol. Monog.* 36: 125-155.
- . 1969. Alpine community patterns in relation to environmental parameters *in* Essays in plant geography and ecology. K. N. H. Greenridge, ed. Nova Scotia Museum, Halifax. pp. 167-184.
- COURTIN, G. 1968. Microclimate of Mt. Washington. *Mt. Washington Observatory News Bulletin* 9: 2-6.
- . 1968a. Evapotranspiration and energy budget of two alpine environments, Mt. Washington, New Hampshire. Ph.D. thesis, Univ. of Ill., Urbana. 172p.
- EDDLEMAN, L. E., E. E. REMMENGA and R. T. WARD. 1964. An evaluation of plot methods for alpine vegetation. *Bull. Torrey Bot. Club* 91: 439-450.
- FERNALD, M. L. 1950. Gray's manual of botany, eighth ed. American Book Co., N.Y. 1632p.
- GLEASON, H. A. and A. CRONQUIST. 1963. Manual of the vascular plants of Northeastern United States and adjacent Canada. D. Van Nostrand Co. Inc., N.Y. 810p.
- GOODALL, D. W. 1970. Statistical plant ecology *in* *Ann. Rev. Ecol. and Syst.*, R. Johnson, P. Frank and C. Michener eds. *Ann. Revs. Inc.*, Palo Alto, Calif. pp. 99-124.
- HADLEY, E. B. and L. C. BLISS. 1964. Energy relationships of alpine plants on Mt. Washington, New Hampshire. *Ecol. Monog.* 34: 331-357.
- HARRIS, S. K. 1964. Mountain flowers of New England. Appalachian Mountain Club, Boston. 147p.
- HOLTTUM, R. E. 1922. The vegetation of West Greenland. *Jour. Ecol.* 10: 87-108.
- HURLBERT, S. H. 1969. A coefficient of interspecific association. *Ecology* 50: 1-9.

- LÖVE, A. and D. LÖVE. 1966. Cytotaxonomy of the alpine vascular plants of Mt. Washington. Univ. Colo. Series in Biol., No. 24. Univ. Colo. Press. 74p.
- PEASE, A. S. 1964. A flora of Northern New Hampshire. New England Botanical Club Inc., Cambridge, Mass. 278p.
- ODUM, E. P. 1971. Fundamentals of ecology, third ed. W. B. Saunders Co., Philadelphia. 574p.
- SAKAI, A. 1970. Mechanism of desiccation damage of conifers wintering in soil-frozen areas. *Ecology* 51: 657-664.
- . and K. OTSUKA. 1970. Freezing resistance of alpine plants. *Ecology* 51: 665-671.
- SAVILLE, D. B. A. 1960. Limitations of the competitive exclusion principle. *Science* 132: 1761.
- SOKAL, R. R. and J. ROHLF. 1969. Biometry. W. H. Freeman & Co., San Francisco, Calif. 776p.
- TRANQUILLINI, W. 1964. The physiology of plants at high altitudes. *Ann. Rev. Plant Physiol.* 15: 345-362.
- WOODIN, H. E. 1959. Establishment of a permanent vegetation transect above timberline on Mt. Marcy, New York. *Ecology* 40: 320-322.

BIOLOGY DEPARTMENT

UNIVERSITY OF MASSACHUSETTS — BOSTON

100 ARLINGTON STREET, BOSTON, MASS. 02116